**REVIEW**

# Migratory connectivity of Palearctic-African migratory birds and their responses to environmental change: the serial residency hypothesis

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In most long-distance migratory birds, juveniles migrate without their parents, and so are likely to lack detailed knowledge of where to go. This suggests the potential for stochasticity to affect their choice of wintering area at a large scale (>1000km). Adults, in contrast, may re-use non-breeding sites that promote their survival, so removing uncertainty from their subsequent migrations. I review the evidence for large scale stochastic juvenile site selection followed by adult site fidelity, and then develop a 'serial-residency' hypothesis based on these two traits as a framework to explain both the migratory connectivity and population dynamics of migrant birds and how these are affected by environmental change. Juvenile stochasticity is apparent in the age-dependent effects of weather or experimental displacement on the outcome of migration and in the very wide variation in the destinations of individuals originating from the same area. Adults have been shown to be very faithful to their wintering grounds and even to staging sites. The serial residency hypothesis predicts that migrants that show these two traits will rely on an individually unique but fixed series of temporally and spatially linked sites to complete their annual cycle. As a consequence, migratory connectivity will be apparent at a very small scale for individuals, but only a large scale for a population, and juveniles are predicted to occur more often at less suitable sites than adults, so that survival will be lower for juveniles. Migratory connectivity will arise only through spatial and temporal autocorrelation with local environmental constraints, particularly on passage, and the distribution and age structure of the population may reflect past environmental constraints. At least some juveniles will discover suitable habitat that they may re-use as adults, thus promoting overall population level resilience to environmental change, and suggesting value in site-based conservation. However, because migratory connectivity only acts on a large scale, any population of a migrant will contain individuals that encounter a change in suitability somewhere in their non-breeding range, so affecting average survival. Differences in population trends will therefore reflect variation in local breeding output added to average survival from wintering and staging areas. The latter is likely to be declining given increasing levels of environmental degradation throughout Africa. Large scale migratory connectivity also has implications for the evolutionary ecology of migrants generally because this is likely to lead to selection for generalist traits.

47 The causes of current population declines of many migrant species in the Palearctic are likely to be
48 both species- and population-specific (Vickery *et al.* 2014), yet a general decline in most migrant
49 species has been recorded over large areas of the Palearctic (European Bird Census Council 2012).
50 If declines in migrants are species- and population-specific, then some characteristics such as their
51 life history strategy or environmental conditions in Africa are likely to be causing the decline recorded
52 across species (Sanderson *et al.* 2006). Here I propose two traits of migrants that may help to explain
53 these population dynamics. First, in most long-distance migrant birds, juveniles migrate without their
54 parents, and most likely lack detailed knowledge of where to go, suggesting the potential for
55 stochasticity to affect their choice of wintering area on a large scale (>1000km). Second, adults then
56 show very high fidelity to these sites, re-using sites that secured their survival as juveniles and so
57 removing uncertainty from their subsequent migrations and location of wintering sites. Here I review
58 the evidence for stochastic juvenile site selection at a large spatial scale, and adult site fidelity, and
59 develop from this a 'serial-residency' hypothesis based on these two traits that forms a framework to
60 explain both the connectivity of migrant species to their wintering grounds and their population
61 dynamics, and how both may vary with environmental change.

62 ***STOCHASTIC LOCATION OF WINTERING SITES BY JUVENILES***

63 The demonstrated ability of migratory birds to return exactly 'home', quickly and efficiently, after a
64 considerable experimental spatial displacement (Mewaldt 1964, Akesson 2003) indicates that birds
65 can be considered to have the equivalent of a GPS system (Thorup *et al.* 2007a, Thorup & Holland
66 2009). Navigation can only take place, however, when the final destination is known but there is no
67 evidence to date of genetic programs that provide naïve migrants with instructions on how to reach
68 wintering sites at a specific location on a small (<100 km) or medium scale (100 – 1000 km). Genetic
69 control of migratory direction in juveniles has been shown to operate only on a very large scale at the
70 level of migratory divides, such as south-west through Iberia or south-east through the Middle East
71 (Perez-Tris *et al.* 2004, Ilieva *et al.* 2012), or with respect to the approximate timing of encounter with
72 barriers which require pauses for refuelling or very major shifts in direction (e.g. Chernetsov *et al.*
73 2008). Migration departure directions are sufficiently variable within individuals to result in large
74 differences in destinations over journeys of several thousand kilometres (Thorup *et al.* 2007b) and
75 within populations (Karlsson *et al.* 2010), and juveniles do not usually use environmental cues to

contradict their basic 'compass and clock' program (e.g. Deutschlander *et al.* 2012, Holland & Helm 2013). Even when they do (e.g. magnetic cues; Kullberg *et al.* 2003), this is again variable across individuals in timing and direction.

Lacking innate small or medium-scale location information, a juvenile bird can only head in the direction of migration and encounter sites stochastically along its line of travel, although as sites are encountered, their location can be learned and so used or avoided in subsequent migrations. Some birds may use social learning to locate suitable passage and wintering sites. Long-lived migrants, for example, will have greater opportunities for removing stochasticity in site selection, leading to extreme cases where social learning may be involved to ensure the same, best sites are always used even by first-year birds (Mueller *et al.* 2013). Some shorter-lived passerine migrants that migrate diurnally in flocks, such as Barn Swallows *Hirundo rustica*, might also use social learning or public information to locate good passage sites and roosts. However, many species show no association between juveniles and adults in the migration period, and indeed many adults migrate before juveniles, so precluding any chance of social learning of destinations from parents. Such species, including almost all passerines where this is known, migrate at night, often singly or in associations formed by bottlenecks on the migration route, but without any coherent, coordinated group behaviour that might suggest some individuals are following others, or have the potential systematically to follow others (Berthold 2001). Although grouping, for whatever reason, must provide an opportunity for individuals to follow one another, we know of no mechanisms whereby such grouping leads to coordinated site selection at medium or small scales. Adults tend to have a different moult and migration phenology, with juveniles travelling more slowly (e.g. Strandberg *et al.* 2008, Hope *et al.* 2011), so making the option of following adults difficult. Nonetheless, studies on the use of cues such as flight calls and adult presence and density, during and at the end of migration, are needed to determine the degree to which any stochasticity might be offset by social information.

### *Evidence for stochastic site selection by juveniles*

Juveniles, unlike adults, do not correct for experimental displacement during migration, thus ending up in atypical wintering areas, whereas adults are able to make corrections and so reach their usual winter quarters (Perdeck 1958, 1967, Wolff 1970). A recent meta-analysis of orientation in caged juvenile birds after displacement has confirmed that any corrections by juveniles in autumn are

105 approximate and even these are probably reliant on star positions in clear skies, whereas juveniles
106 returning in the spring correct more coherently as if heading back to their known breeding grounds
107 (Thorup & Rabol 2007). Experienced birds, in contrast, use 'true navigation' whereby celestial and
108 magnetic cues along with site-specific experience allow for precise orientation and correction after
109 displacement (Wiltschko & Wiltschko 1999).

110 Many migrants may use favourable tailwinds during migration (Erni *et al.* 2005). This implies that
111 change in wind direction during a migration flight, or slight differences in starting wind directions, can
112 influence destinations. Although compensation for this wind drift can occur, it is species- and context-
113 specific (Liechti 2006) and can result, after strong, sustained and unexpected winds, in very large
114 numbers of birds, notably passerines, being displaced from their usual migration paths (Elkins 1983).
115 Passerines, in particular, may also migrate without favourable tailwinds because they are time-
116 constrained and so are likely to be subject to small changes in direction as a result of wind drift
117 throughout every night of their long-distance migrations (Karlsson *et al.* 2011). Consequently, even if
118 genetic orientation mechanisms of juveniles were more precise, accumulated small deviations over a
119 long migration will result in destinations that vary on a country-wide scale (Mouritsen 2003).

120 Wintering locations of individuals are now becoming better known from light-based geolocators and
121 satellite telemetry, and this evidence suggests that there is wide variation in the wintering destinations
122 of individuals originating from the same population (Table 1). The wintering distributions of individuals
123 from the same small breeding area in Europe may extend over thousands of kilometres in Africa.
124 However, the measurement of migratory tracks of small passerine species from such tags is in its
125 infancy, and hence biased against finding connectivity because of the stochasticity inherent in small
126 sample sizes. Many more data are needed and will emerge as tagging capability and programs
127 expand.

128 Further evidence that juveniles reach their wintering sites stochastically is that they occur commonly
129 in any habitat that is minimally suitable (e.g. Nevoux *et al.* 2008), and not always in the best habitats.
130 Evidence is limited, but one study of Eurasian Spoonbills *Platalea leucorodia* has been able to
131 examine this over a convincing scale that accounted for dispersal as well as survival, finding that
132 Spoonbills were highly faithful to winter sites despite others being available that would result in higher
133 survival (Lok *et al.* 2011). There same has been found for Icelandic Black-tailed Godwits *Limosa*
134 *limosa islandica* wintering in Western Europe (Gunnarsson *et al.* 2005). Similar evidence comes from

a lack of correlation between settlement patterns of migrants and the quality of sites (e.g. Johnson *et al.* 2009, 2011).

### *Post-migration sampling of sites to compensate for stochasticity*

On arrival, subsequent movements may then occur so that the stochasticity of migration can be mitigated by finding better sites locally. Although little is known about the degree of local, post-migratory sampling undertaken by juvenile birds (Mettke-Hofmann & Greenberg 2005), we may gain some insight by examining dispersal distances from the natal site on return at after the first complete migration. Although these distances are likely to be underestimated in many studies (e.g. c. 1-10 km, Sutherland *et al.* 2000), mean distances analysed from population demographic methods for passerines are of the order of 15-95 km (Tittler *et al.* 2009). This scale is compatible with the stochastic nature of juvenile migratory destinations at a medium to large scale. Any migrant, when necessary, may carry out site selection at larger scales to compensate for stochasticity (e.g. Honey Buzzards *Pernis apivorus* Strandberg *et al.* 2012). Nevertheless this does not mean that many do, because the advantages of locating the best site may not outweigh the costs of moving on a large scale or delaying site selection.

Key to understanding the stochasticity involved in selection of a wintering site by juveniles are the relative costs and benefits of moving. If these are high and low respectively, then juveniles should invest little time and energy in sampling sites and stay roughly where they initially settle in Africa (Switzer 1993). There is some evidence that costs of moving between sites are high. Migration itself incurs a survival cost (Strandberg *et al.* 2010), whereas juveniles that have become resident on a site for the winter have the same survival as adults (Sillett & Holmes 2002), suggesting that movement between sites results in lower survival than residency. Mechanisms for increased cost are likely to include increased predation risk in unfamiliar surroundings (e.g. Clarke *et al.* 1993, Yoder *et al.* 2004) and increased encounter rates with new parasites (Møller & Szep 2011).

There is also some evidence to suggest that the benefits of switching sites at a large scale may be low, at least for Palearctic passerine migrants wintering in Africa because suitable, unoccupied habitat is widespread. First, the absence of Palearctic migrants from certain wintering habitats is well predicted by habitat models but, within suitable habitat, presence is poorly predicted, suggesting that much suitable habitat is unoccupied (Wilson & Cresswell 2006, Cresswell *et al.* 2007, Hulme &

Cresswell 2012). Second, many Palearctic terrestrial migrant species occur in a wide range of habitats (Rabøl 1987, Leisler 1990, Morel & Morel 1992, Pearson & Lack 1992, Salewski & Jones 2006). Some studies in the Neotropics suggest the opposite, with clear survival differences between habitats and evidence of exclusion of age and sex classes (Strong & Sherry 2000, Marra & Holmes 2001). However, habitat limitation, and indeed many factors which affect migrants, may act differently in the Neotropics because many species winter in Central America and on Caribbean islands where the availability of land is limited (Jones & Cresswell 2010).

A further key issue in understanding the net costs of sampling and moving between sites lies in the concept of predictability of foraging and management of hazard such as predation risk (Cuadrado 1997), both of which rely on local information. The information needed to allow prediction of foraging gain and management of starvation and predation risks can only be gained through experience of a site. Therefore the value of a site increases with greater residence in it (Piper 2011). This concept perhaps explains why migration for first-year birds (and adults that have their migratory routes disrupted by weather) carries greater survival costs (see below). Each step means that a new site must be sampled and assessed, to gain knowledge of local food sources, competitor densities, predators and the location of refuges, which will interact to determine predation risks and foraging predictability (Lind & Cresswell 2006, Cresswell 2011). The process of gaining experience of a site may itself increase energetic costs, reduce foraging time and increase predation risk for migrants (see Robinson & Merrill 2013 for a mammalian example of this). If much of the cost of shifts between sites in wintering areas is a consequence of imperfect information, then we would predict that birds select wintering sites according to a threshold of minimum acceptability to reduce the time to locate a site (see Oring 1982 for this argument applied to breeding territories). This is made more compelling by considering that the energy requirements of a passerine in the tropics are relatively low outside migration periods and foraging may only need to occur for a few hours every day (Brandt & Cresswell 2009). A migrant in a poor site might choose simply to feed for longer during the day rather than risk seeking a better site.

A further consideration in determining the scale at which winter site selection is stochastic is the degree to which juveniles use the presence of adults in an area to locate suitable habitats. Once a juvenile arrives in a potential wintering area it may then locate suitable wintering sites at a finer scale using local enhancement, whereby the presence of adult conspecifics indicates suitable and probably

high quality habitat. Conspecific attraction certainly occurs in choice of breeding site when the confounding effect of habitat quality itself is experimentally removed (e.g. Hahn & Silverman 2006, Betts *et al.* 2008, Theriault *et al.* 2012). We know nothing of whether birds use local enhancement to locate suitable wintering areas, but it seems reasonable that they would do so and consequently aggregate depending on a pre-existing distribution.

## NON-BREEDING SITE FIDELITY IN ADULTS

There is much convincing evidence of site fidelity to the main non-breeding sites (wintering sites where individuals spend more than a few days) for many of the migrant species for which data are available (Table 2 and Newton 2008). Site fidelity in birds generally seems to vary along a continuum from highly site-faithful even at a small spatial scale, to virtually no fidelity at any scale, depending on year-to-year predictability in food-supplies (Newton 2008). Serial residency and its associated predictions will have much less relevance to any population that specialises on spatially unpredictable food supplies or ephemeral habitats (Newton 2012) such as White Storks *Ciconia ciconia* (Berthold *et al.* 2002). However, there is no evidence that any Palearctic-African passerine migrant is nomadic (i.e. sudden appearances in non-usual areas of large numbers of individuals), and in non-passerines such as raptors and storks nomadism is perhaps much more noticeable and easier to demonstrate than serial residency. This is distinct from the use made by individuals of several species of more than one wintering site (or prolonged staging sites) in Africa (Jones 1995). These typically reflect large-scale movements in response to worsening dry season conditions as a consequence of intra-annual rainfall and primary productivity patterns (Tottrup *et al.* 2012, Lemke *et al.* 2013). There is no logical reason to suppose that use of several wintering sites would affect fidelity to any one of these sites, but there are no data available to examine this.

Fidelity to passage sites, where individuals may only spend a few days refuelling before continuing migration, has not been as well demonstrated for passerines. Fidelity to staging sites may be lower because it is harder for birds to assess the quality of a particular staging site given that they only sample it for a short period of time, and there may be greater short-term temporal variation in competitor numbers at staging sites than at over-wintering sites (G. Ruxton pers. comm.). Nevertheless, some geese, shorebirds and raptors have high site fidelity to passage sites (Table 2

223 and Newton 2008), even though apparent site fidelity may be inflated by limited availability of suitable
224 staging sites. Most passerines probably do not have site fidelity for passage sites (Catry *et al.* 2004),
225 but it does occur in some species (Table 2, Newton 2008).

226 What is known about wintering site fidelity is entirely consistent with what we know about breeding
227 site fidelity. Breeding and natal site fidelity at a very small scale (hundreds of metres) in most adult
228 birds, and at a slightly larger scale (<10 km) in juveniles, has been long established (Greenwood &
229 Harvey 1982). Although there are many exceptions, and the degree of site fidelity is dependent on
230 many ecological factors, most birds tend breed close to their natal site. Much of the contention about
231 whether or not species are site-faithful is actually about the scale of dispersal (Cilimburg *et al.* 2002,
232 Hosner & Winkler 2007). Natal and breeding site fidelity of migrants in particular is well established
233 and tends to be similar to that of non-migratory populations or species (Greenwood & Harvey 1982,
234 Sandercock & Jaramillo 2002, Middleton *et al.* 2006, Foerschler *et al.* 2010) and between migrants
235 occupying different habitats (Schlossberg 2009).

236 What we know about wintering and breeding site fidelity predicts that an individual migrant is likely to
237 occupy the same sites for breeding and wintering throughout its life, even over many years (hence
238 'serial' residency), and this may also extend to the passage stop-over sites between them. This does
239 not, however, rule out an individual abandoning sites or adopting new sites, or using multiple
240 wintering sites but, on average, if sites remain available and suitable, the prediction is that they will be
241 used again. Site fidelity is expected to decrease with increase in variation at sites due to changes in
242 weather, climate, habitat and competition, or the ability of a migrant species to find and move to better
243 sites. As with juveniles, the key to understanding adult site fidelity is therefore the cost of changing
244 habitat and the scale over which site changes occur (see Møller & Szep 2011 for an example
245 involving the costs of parasitism leading to selection for winter site fidelity). However, there is little
246 information available to examine how frequently and why adult birds change their wintering sites.

247 We have much better information for change of breeding site, and it may be that similar rules apply for
248 shifts to new wintering sites. Adult birds tend not to change breeding sites, particularly as they get
249 older and more experienced (Middleton *et al.* 2006, Sergio *et al.* 2009, Bernard *et al.* 2011), and when
250 they do so movements are generally <100km. Many studies show shifts in breeding sites over
251 relatively small distances (of the order of <1-10km) and usually only females move in response to
252 reduced reproductive success (Sedgwick 2004, Eeva *et al.* 2008, Schaub & von Hirschheydt 2009).

However, many studies that show such correlations between site shifts and reproductive success are confounded by increasing reproductive success with age. Thus, when experimental manipulations of reproductive success are carried out these tend not to lead to site shifts (e.g. Howlett & Stutchbury 2003, Shutler & Clark 2003, but see Hoover 2003). Studies that experimentally manipulate habitat quality to induce movements to new areas have not been carried out for any migrant species on the wintering grounds in Africa, and there are real biases towards not identifying species that have low site fidelity because of the scale of study necessary. Nevertheless the expectation of high adult site fidelity on even a small scale seems the most parsimonious for wintering passerines.

## THE SERIAL RESIDENCY HYPOTHESIS

Traits whereby large (>1000 km) and probably medium (>100 km) scale location of passage and wintering sites is stochastic by juveniles on first migration, but then surviving adults have high site fidelity to the wintering and possibly also staging sites in subsequent migrations, form the basis of a novel 'serial residency' hypothesis. This hypothesis generates testable predictions in three areas:

(i) ***Age-dependent site use and survival***. Juveniles are predicted to show greater variance of migration routes and number of stop-over sites in time and space, and greater occurrence than adults at less suitable sites, so that survival is higher for adults than juveniles.

(ii) ***Migratory connectivity***. This will arise only through spatial and temporal autocorrelation of local environmental constraints, particularly on passage, and the distribution and age structure of the population may reflect past environmental constraints.

(iii) ***Population resilience***. At least some juvenile birds will discover suitable habitat that can be re-used when the birds are adults, allowing overall population level resilience to environmental change and giving value to site-based conservation.

The serial residency hypothesis is most likely to apply to species in those orders of birds (e.g. Passeriformes) of smaller body size, lower flight range and lower ability to maintain migration and orientation in adverse weather. Such birds are subject to events during migration that cannot be predicted or compensated for, and end up distributed over a wider area when they reach their wintering grounds. The hypothesis will apply less to those orders with characteristics such as large

body size, high flight speeds and large flight ranges such as shorebirds, swifts and terns, or with social learning, such as wildfowl and cranes. In these cases, most species may use initial large scale sampling of sites or public information to end up in targeted areas.

Under the serial residency hypothesis, stochastic site selection, site fidelity and resultant migratory connectivity are all scale-dependent. At a small scale – within a few hundred metres to less than 10 kilometres – any species may sample or use social information to choose sites in a non-random fashion and this may even extend to 10 – 100 km. However sampling of or ability to choose sites on a larger scale (greater than 100 km) is much less likely to occur, so at this scale, site choice may be stochastic. Similarly, at a very large scale (greater than 1000 km) there is always migratory connectivity (i.e. western Europe to west Africa).

***Age-dependent site use and survival***

Juveniles are predicted to show greater variance of migration routes and number of stop-over sites in time and space, and greater occurrence at lower quality sites, because they lack knowledge and migration arrival location is stochastic. The degree to which a migrant will show predictable site re-use in time and space across years within a species is also then modified by its age. As birds age we expect them to become more site faithful, both because of natural selection removing those that have not located suitable sites and because the value of a site probably increases with experience of it. Moreover, any necessary shifts in sites have already been made earlier in life. Survival is therefore predicted to be higher for adults than juveniles. Juvenile survival has been universally found to be lower than adult survival in migrants (e.g. Sæther 1989, Donovan *et al.* 1995, Sæther & Bakke 2000), but the underlying mechanisms predicted by the serial residency hypothesis remain to be tested.

***Migratory connectivity***

Migratory connectivity is predicted to arise through spatial autocorrelation because populations from the same area experience similar local constraints and so follow the same migration routes (Fig. 1). Although selection of wintering sites for juveniles is predicted to be stochastic, local environmental factors will constrain survivable routes and so influence and limit the potential outcomes. For example a terrestrial migrant cannot find a wintering site if it ends up migrating too far to the west into the Atlantic. Consequently we predict migratory connectivity as a consequence of these limitations (e.g. Cano & Telleria 2013). This is particularly relevant to any comparisons between the Nearctic and

310 Palearctic migration systems because of the much smaller land availability in the former system:
311 migratory connectivity will be very much greater in the Nearctic even if the serial residency hypothesis
312 applies equally.

313 Distribution patterns in Africa (and so migratory connectivity) may also reflect past history,
314 environmental and cohort events. Initially, stochasticity and the costs of finding the best sites may
315 lead to selection of non-optimal sites by juveniles. Then inter-annual or decadal changes in local
316 climatic conditions on the wintering grounds – well recorded in Africa (Nicholson 2001) - may lead to
317 changes in the quality of these sites for the returning adults, which may return to the same site for
318 several years (Fig. 1). Consequently bird-habitat associations on the wintering grounds may be weak
319 (e.g. Wilson & Cresswell 2006, Cresswell *et al.* 2007, Hulme & Cresswell 2012). Furthermore, in years
320 in which the best sites for winter survival change there will be a greater proportion of juveniles
321 surviving to breed the following year, because adults become concentrated where conditions were
322 suitable previously (due to differential survival) whereas juveniles always end up over a wider area
323 (Fig. 1, panels iii & iv). For example, the serial residency hypothesis would predict that there would
324 have been a greater proportion of juvenile Common Whitethroats *Sylvia communis* returning to
325 western Europe in 1969, after the likely major change in typical habitat conditions in the Sahel during
326 the previous winter caused a >50% reduction in the size of the returning population (Winstanley *et al.*
327 1974).

328 A further possible influence on connectivity may arise through the use of more than one main
329 wintering site in Africa. Although stochasticity in initial site selection will apply independently of the
330 number of wintering sites, we know little about whether shifts between wintering sites are a gradual
331 drift south as conditions worsen (e.g. Cresswell *et al.* 2009), or represent a single-step flight (e.g.
332 Lemke *et al.* 2013). Gradual shifts southward would be more likely lead to fine scale optimal habitat
333 selection which would be perhaps more significant for the end of the winter when body condition
334 needs to be prioritised for migration back to Europe. Increased population level connectivity might
335 then result as birds concentrate in the best areas later in the winter. In contrast, intra-African migration
336 during the winter to a new site would be likely to lead to further stochasticity (again juveniles will not
337 know where they are going) and so further reduce population level connectivity. It is interesting to
338 note that the one Palearctic passerine migrant species that has been shown to have an intra-African
339 migration during the wintering period has also been shown to have the largest spread in wintering

destinations from a single breeding site and so the lowest migratory connectivity (Lemke *et al.* 2013, Table 1).

***Population resilience***

If a migrant bird shows serial residency, then it will rely on a series of individually unique, connected sites in both space and time. The dependence on a chain of sites makes an individual migrant relatively more vulnerable to change because the probability that any one site is affected by environmental change increases with the number of sites used - 'multiple jeopardy' (Newton 2004). Populations in which individuals have more stop-over sites will therefore be more likely to show declines than those with fewer. The average number of stop-over sites for most species is unknown and, although migration distance may be a proxy, inter-specific variation in migratory capability and the availability of stop-over sites due to variation in average routes will confound this. Both passerine and non-passerine species with longer migration distances to Africa have been shown to have suffered larger declines (Sanderson *et al.* 2006, Møller 2008, Jones & Cresswell 2010), but regardless of the number of sites used, loss of one may have the same effect, so that even shorter-distance migrants will be affected by the loss of key sites. It is also important to note that there may be circumstances when use of multiple sites increases fitness in a migrant, because it might allow better adjustment of migratory timing (see below) or a bet-hedging strategy in the context of optimal migration (Alerstam *et al.* 1990, Alerstam 2011).

The serial residency hypothesis, however, modifies the predictions of the 'multiple jeopardy' hypothesis because it predicts that there will be intraspecific spatial and temporal variation in which stop-over sites are used rather than simply just considering their number. Because initial discovery and use of each site by juveniles is largely stochastic and untargeted except at a broad spatial scale, each adult is likely to have a different series of linked sites. Therefore increased resilience at a population level emerges as a prediction, for any given average number of sites used by a migrant species. At least some first-year birds will discover functional links that can be re-used as adults, including protected areas. These links will be different even within populations so that environmental change will usually only affect some individuals of the population in any one year. Therefore, the serial residency hypothesis predicts that populations with greater first-year stochasticity in route

finding will be more resilient to larger scale change (i.e. there will always be some first-year individuals that find a functional linked chain of sites). These predictions have not been tested to date.

The extent of population resilience engendered by serial residency is however dependent on whether environmental conditions limit availability of passage sites at any stage (i.e. migratory bottlenecks) and on the spatial scale of environmental change. Populations that are concentrated at sites because of bottlenecks will be more susceptible to anthropogenic change even if they otherwise follow the predictions of the serial residency hypothesis. Large population declines have been shown to be associated with bottlenecks (Baker *et al.* 2004, Verkuil *et al.* 2012), but in most cases we do not know the degree to which most populations are concentrated into bottlenecks. Habitat specialisation will be a proxy for this however, and species that are habitat specialists have been shown to have suffered larger declines (Siriwardena *et al.* 1998, Gregory *et al.* 2004, 2007, Hewson *et al.* 2007). Additionally, where change is operating over a large spatial scale, such as climate change, then most individuals in a population might be affected, despite a wide spatial separation in sites and routes.

## Understanding and managing Palearctic passerine migrant declines

Testing the predictions of the serial residency hypothesis will allow us better to understand why many European passerine migrant bird species are declining, but in a very population-specific way. If there is initial stochasticity of juvenile site selection on the wintering grounds such that there is only migratory connectivity on a very large scale, then conditions throughout the wintering grounds affect all breeding populations of a species (Taylor & Norris 2010). Some juveniles from a population end up in good sites and others in poor sites, with average survival reflecting the relative availability of good and poor sites across the African wintering range. Average juvenile survival over a very large scale is then added to the breeding productivity of a population in an area of Europe being monitored on a much smaller scale to give overall population change. Thus whether a particular breeding population is declining, static or increasing may depend on the quality of the environment on the scale that the population is being monitored in Europe, but the proportion of local populations that are declining, static or increasing, may depend on the average quality of the environment over the whole wintering area (Fig. 2). So as average environmental quality throughout Africa decreases (e.g. Lutz & Samir 2010), so the overall population trend for a migrant species is predicted to become more negative at larger (e.g. European) scales. Consequently we may have highly variable population dynamics for

migrant species within Europe depending on country or area in which they breed, but an overarching effect of quality of the wintering ground. Furthermore, because birds from specific wintering sites are spread over a wide range of breeding sites, local wintering populations have some resilience against destruction of specific breeding sites. Limiting factors which act locally (like piecemeal habitat destruction) may then have less immediate impact on overall populations than factors, such as climatic influences, that act simultaneously over wide areas.

The lack of small- or medium-scale migratory connectivity then has profound implications for any hypotheses about where population limitation in Palearctic migrants occurs (e.g. Newton 2004, Taylor & Norris 2010). Without large-scale connectivity, factors that affect breeding populations for any relatively local scale breeding population monitored in Europe will always have a stronger effect than factors measured at a local scale on the wintering ground. This is because any local detrimental change in Africa will affect a population in Europe by reducing survival of only those individuals that winter in the affected area, so these decreases will be diluted by the many individuals wintering in other areas of Africa not affected by the local change. However, any detrimental change on the breeding grounds in Europe will affect all individuals being monitored, so giving a stronger average effect. The converse would apply if we monitored a wintering population. Any conclusion about the relative strength of population limitation on the breeding and wintering grounds will therefore be influenced by the location and the scale of the study from which it comes (Foppen *et al.* 1999, Morrison *et al.* 2013b). For example, Willow Warblers *Phylloscopus trochilus* in Britain have very different regional population trends (Morrison *et al.* 2010) but have the same wintering regions and habitat requirements (Morrison *et al.* 2013a). Only by comparison of populations, species or functional groups that differ fundamentally in their wintering habitats in Africa (e.g. Sahel vs forest) or have different wintering areas on a very large geographical scale (e.g. east vs west Africa) will population trend differences emerge that can be related to their wintering grounds (e.g. Sanderson *et al.* 2006, Ockendon *et al.* 2012).

We would therefore predict that local breeding parameters would correlate more often, or more strongly, with local breeding population trends than wintering parameters. Taking the ten most declining migrant species in Europe and searching the most recent 150 papers or papers published over a 10-year period on Web of Science using the keywords ‘species name’ and ‘breeding’ or ‘wintering’, eight species were the subject of studies that examined the relative effect of drivers of

local breeding population change. Almost all of these show local breeding parameters as a main driver of local population change, including European Turtle Dove *Streptopelia turtur* (Browne & Aebischer 2004), Wood Warbler *Phylloscopus sibilatrix* (Mallord *et al.* 2012), Willow Warbler (Hogstad 2005), Whinchat *Saxicola rubetra* (Grubler *et al.* 2008), European Pied Flycatcher *Ficedula hypoleuca* (Both *et al.* 2006a), Eurasian Reed Warbler *Acrocephalus scirpaceus* (Harrison & Whitehouse 2012) and Garden Warbler *Sylvia borin* (Widmer 1996). In contrast, only one study showed the dominance of wintering conditions on local population dynamics, in Northern Wheatear (Arlt *et al.* 2008). But it is again important to note that the importance of scale in this argument. As the geographic size of the breeding population considered increases, so the importance of wintering conditions as drivers of breeding population dynamics increases (Baillie & Peach 1992, Thingstad *et al.* 2006).

Stochastic site selection by juveniles at a large scale also has implications for the importance of phenological mismatch (Jones & Cresswell 2010) in driving population dynamics of passerine migrants. Critical to this hypothesis, whereby population declines are predicted because climate change occurs disproportionately in the wintering and the breeding areas such that migrants arrive to breed later than the local food peak, is that cues on the wintering ground may inform breeding arrival times (e.g. Both *et al.* 2006b). If there is little migratory connectivity then it is unlikely that selection can act for the use of winter climate cues to time migration. Only cues that correlate well with habitat suitability across the entire wintering range can have a selective effect (e.g. Saino *et al.* 2007, van Wijk *et al.* 2012). It seems likely therefore that selection will have acted on migrants to use timing mechanisms independent of local climate cues, long before anthropogenic climate change may have disrupted them. Only populations that have clear migratory bottlenecks, or that have greater migratory connectivity because of common wintering or passage sites relatively close to the breeding ground, might be expected to show migratory timing changes in response to breeding climate change (Both & te Marvelde 2007, Both 2010, Rubolini *et al.* 2010, Tottrup *et al.* 2010).

The serial residency hypothesis has clear conservation implications. First, maintenance of a network of protected areas on the wintering grounds will always protect some individuals from all populations in Europe because juveniles redistribute annually, and so this will be the case even with climate change, as long as the network of protected areas overall still embraces suitable habitat (Fig. 2). Second, species with high stochasticity in initial site selection will also have diverse migration routes promoting resilience and the effectiveness of a large network of conserved sites, regardless of

location. Third, any actions which promote the carrying capacity of habitats for such migrants anywhere in Africa will benefit a large range of breeding populations in Europe, although these actions would have to be very widespread to have detectable effects. In contrast, if a species has low stochasticity in site selection then specific local solutions on the wintering grounds will be needed to affect specific local European breeding populations, and identification, management and protection of key wintering sites is then of utmost importance. Such species are also likely to have specific migration routes with key bottleneck passage sites that require identification and conservation, with alternative sites also conserved to insure against future anthropogenic and climate change. These species will therefore be much more susceptible to anthropogenic climate and habitat change but will also respond quickly to targeted local conservation initiatives.

Overall, the most important population implication of the serial residency hypothesis is perhaps that we should expect average changes in conditions across African wintering grounds at a large scale to more or less affect all European passerine migrant populations such that decadal changes in rainfall or habitat change will cause groups of species sharing the same wintering habitats to show consistent population changes. Some of these changes may reflect natural variation in rainfall patterns such as periods of wet and dry in the Sahel, whereas others may reflect long term anthropogenic degradation of wooded and savannah wintering habitats, or key passage sites. Any natural change or conservation action that increases carrying capacity for migrants in suitable habitat in Africa will positively affect Palearctic passerine migrant populations by increasing juvenile survival. However, if the surrounding environment is degraded these local positive effects may be swamped by greater large scale effects on juvenile survival. Therefore we need sustainable development solutions that minimise the large scale average impact that the increasing human population in Africa has on its habitats for migrant birds.

## Conclusion: passerine migrants must be generalists

Serial residency may well be the consequence of selection to provide passerine migrants with a mechanism to deal with the environmental change that we know occurs in Africa on a decadal, and indeed, often an inter-annual basis, due to major variation in rainfall patterns (Nicholson 2001). Therefore we should expect corresponding changes in juvenile survival to affect overall population trends in Europe as part of this ‘natural’ dynamic system. For example, coincident with reduced

rainfall in the Sahel we have observed declines in Sahelian wintering species and these have now reversed as Sahelian rainfall has increased through the last decade. In contrast, species wintering in the Guinea savanna are now considered to have greater declines, where widespread anthropogenic habitat modification is likely to be increasing (Thaxter *et al.* 2010, Ockendon *et al.* 2012). Much of the variation we see in European migrant populations may therefore reflect 'normal' readjustment of the distribution of migrants to climate variation in Africa. This does not mean that we should not be concerned about migrant declines, because any anthropogenic degradation of the environment will always affect European populations. But it does mean that we should always expect some migrant populations to be increasing and some to be decreasing with decadal and even longer term changes in climatic conditions (mainly rainfall variation) across Africa. We should also expect large decadal changes in the distribution of Palearctic migrants in Africa to reflect these decadal changes in climatic conditions. This may well be the case, as is hinted at by likely changes in distribution of the main wintering and staging areas of Common Whitethroats during the last 40 years (Winstanley *et al.* 1974, Vickery *et al.* 1999, Wilson & Cresswell 2006), although our information on distribution in west Africa is at such poor temporal and spatial resolution that we would be unlikely to detect even very large scale changes in distribution.

The serial residency hypothesis has implications for the evolutionary ecology of passerine migrants generally, because if migratory connectivity only occurs at a large scale, then this is likely to lead to selection for generalist traits. Those individuals in a population that are able to exploit a wide range of habitats and conditions on the wintering grounds or during migration will be at a selective advantage because their initial post-migration sites are likely to be more suitable than those of specialists. As has been discussed above, there is evidence to suggest only weak co-variation of Palearctic migrant density with habitat quality in Africa, and studies that have explored foraging or inter-specific competition in Palearctic migrants in Africa have by and large described generalist traits (Salewski *et al.* 2003, Wilson & Cresswell 2007, Jones *et al.* 2010, Wilson & Cresswell 2010). There will also be selection with respect to ability to deal with the increased range of environmental conditions encountered (e.g. Møller & Szep 2011). Finally it has been suggested that higher within-clutch variation of migratory orientation compared to within-clutch homogeneity may yield higher geometric mean fitness in migratory populations (Reilly & Reilly 2009) suggesting that a generalist 'bet-hedging' strategy in migrants is fundamental.

The degree to which a migrant species has fidelity to a site initially located stochastically, and the scale at which the stochasticity operates, will determine whether the predictions outlined here apply. Therefore there is a clear priority for research to enable identification of those species to which the serial residency hypothesis applies. In general, we would expect it to apply wherever a species is generalist and associated with wintering habitats that shift in space and time over a period of decades. Then, the key research area is juvenile site selection and survival. Currently, these parameters are inadequately monitored because variable natal site fidelity confounds estimates of true survival of birds over the first winter. Nevertheless, losses between fledging and the following breeding season, when estimated, have been shown to be important in the population dynamics of many migrant species (Baillie & Peach 1992, Newton 1998). In particular, we need studies of how the initial degree of stochasticity in site selection by juveniles affects survival and how wintering habitat quality affects survival of migrants in their wintering area.

In conclusion, the serial residency hypothesis provides a framework to explain many of the population dynamics of passerine migrant birds, and perhaps those of many non-passerines. Two simple rules that are reasonably supported by empirical evidence lead to a large number of predictions that are, when they have actually been tested, supported by further empirical evidence. But perhaps the most important implication is that serial residency is a migratory strategy that must have evolved to deal with environmental change: it allows some individuals from a brood to survive even in spatially unpredictable environments. Therefore we might always expect high levels of variation in migrant population trends and their distribution, particularly within the highly dynamic context of environmental change in Africa.

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933 **Table 1.** Spread of tagged individuals on their wintering grounds.

| Species | Origin | Winter range (km) | Countries (E to W) | N | Study |
|---|---|---|---|---|---|
| Black Stork<br>*Ciconia nigra* | Central Iberia | 3200 | Senegal<br>Chad | 6 | (Cano & Telleria 2013) |
| Cinerous Vulture<br>*Aegypius monachus* | Caucasus | 1400 | Saudi Arabia<br>Oman | 6 | (Gavashelishvili *et al.* 2012) |
| Western Marsh Harrier<br>*Circus aeruginosus* | Sweden | 1100 | Guinea Bissau<br>Mali | 17 | (Strandberg *et al.* 2008) |
| Eurasian Hobby<br>*Falco subbuteo* | Sweden | 1400 | DR Congo<br>Angola | 3 | (Strandberg *et al.* 2009) |
| European Nightjar<br>*Caprimulgus europaeus* | UK | 900 | Central Africa | 3 | (Cresswell & Edwards 2012) |
| Eurasian Hoopoe<br>*Upupa epops* | Switzerland | 1300 | Mauritania<br>Mali | 3 | (Bächler *et al.* 2010) |
| Red-backed Shrike<br>*Lanius collurio* | Denmark | 1400 | Angola<br>South Africa | 9 | (Tottrup *et al.* 2012) |
| Common Redstart<br>*Phoenicurus phoenicurus* | Denmark | 1650 | Senegal<br>Burkina Faso | 6 | (Kristensen *et al.* 2013) |
| Great Reed Warbler<br>*Acrocephalus arundinaceus* | Sweden | 3250 | Guinea<br>CAR | 8 | (Lemke *et al.* 2013) |

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935 **Table 2.** Examples of studies showing evidence of winter and passage site fidelity for long distance
936 migrant bird taxa. Evidence for wintering (W) site fidelity shown top (pale grey) arranged in order of
937 strength of evidence, followed by passage (P) site fidelity shown below (darker grey) again arranged
938 in order of strength of evidence. Te = Temperate and Tr = Tropical. Further studies of migrants that
939 present evidence prior to 2002 are detailed in Table 17.6 in Newton (2008).

| Taxa | Location | Evidence | Source |
|---|---|---|---|
| Passerine | W, Te | Return after experimental displacement | (Mewaldt 1964, Benvenuti & Ioalè 1980) |
| Passerine | W, Tr & Te | Very high fidelity | (King & Hutchinson 2001, Marra & Holmes 2001, Sillett & Holmes 2002, Seavy *et al.* 2012) |
| Waterfowl | W, Te | Most species very high fidelity | (Iverson *et al.* 2004, Iverson & Esler 2006, Liu *et al.* 2012) |
| Spoonbill | W, Tr | Very high fidelity despite non-optimal sites | (Lok *et al.* 2011) |
| Raptor | W, Tr | Small, medium and large scale fidelity | (McGrady *et al.* 2003, Hinnebusch *et al.* 2010, Kochert *et al.* 2011, Gavashelishvili *et al.* 2012, Liminana *et al.* 2012, Trierweiler *et al.* 2013) |
| Seabird | W, SO | Large and medium scale non-breeding fidelity | (Phillips *et al.* 2005) |
| Shorebird | W, Tr, Te | Very high small scale fidelity | (Leyrer *et al.* 2006, Ferreira Rodrigues *et al.* 2007, Conklin & Battley 2012) |
| Passerine | W, Tr | Anecdotal fidelity, many species | (Moreau 1969) |
| Passerine, Raptor | W (P), Tr | Serial fidelity at more than one wintering site during a winter | (Hedenström *et al.* 1993, Heckscher *et al.* 2011, Liminana *et al.* 2012) |
| Passerine | W, Tr | Several species, high but species-dependent variable fidelity | (Faaborg & Arendt 1984, Warkentin & Hernández 1996, Jahn *et al.* 2009) |
| Passerine | W, P, Te, Tr | Migratory connectivity through stable isotopes | (Yohannes *et al.* 2007, Prochazka *et al.* 2008, Studds *et al.* 2008, Yohannes *et al.* 2008) |
| Passerine, Shorebirds | P, Te, Tr | High site fidelity on passage sites established | (Merom *et al.* 2000, Buchanan *et al.* 2011) |
| Raptor, Owls | P, Te, Tr | Site fidelity on medium scale | (Strandberg *et al.* 2008, Beckett & Proudfoot 2011) |
| Shorebird, Passerine | P, Te, | Possibility of high fidelity demonstrated | (Taylor & Bishop 2008, Somershoe *et al.* 2009) |
| Passerine | P, Te, Tr | Several species, little fidelity | (Catry *et al.* 2004, Stanley *et al.* 2012, Vogt *et al.* 2012) |
| Stork, Raptor | P, Te | No site fidelity on medium scale | (Alerstam *et al.* 2006, Chevallier *et al.* 2011, Liminana *et al.* 2012) |

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## Figure legends

**Figure 1**. Population predictions from the serial residency hypothesis. Diagrams illustrate how migratory connectivity arises through spatial and temporal autocorrelation of local environmental constraints (i & ii), how age structure of the population can change with inter-annual shifts in wintering conditions (iii & iv) and how site-based conservation can function as a strategy despite stochasticity (iii & iv). A hypothetical breeding area (grey and B1-3) and a hypothetical wintering area (white and W1-3) are shown. Wintering migratory pathways are shown as arrows linking the breeding areas with the wintering areas. In (ii) migratory connectivity differences arise because of the presence of barriers constraining wintering migratory pathways. In (iii) adults survive preferentially because they always return to the best areas (W1), while many juveniles end up in poor areas. In (iv) the best areas have shifted between years so many adults return to the now poorer areas and have lower survival whereas juveniles arriving to the new best areas (W2) survive better: consequently the age ratio shifts on the breeding ground the following year. Regardless of the shifting location of ideal conditions (iii & iv), as long as some sites within suitable wintering areas are protected (dark circles) then some juveniles will find the sites and return there as adults.

**Figure 2.** A theoretical illustration of how variable conditions on the breeding ground (left hand, summer, graphs showing the effects on population trends through time) add to the uniform, average effects on the wintering ground (middle, winter graphs showing the effects population trends through time) to give the overall population trends over time (right hand graphs). All breeding populations winter right across the southerly wintering grounds and so all will have lower juvenile survival, leading to similarities in trends across these populations, unless these are offset by greater variation in breeding demographics, potentially leading to distinct differences in trends between breeding populations.

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967 Fig. 1
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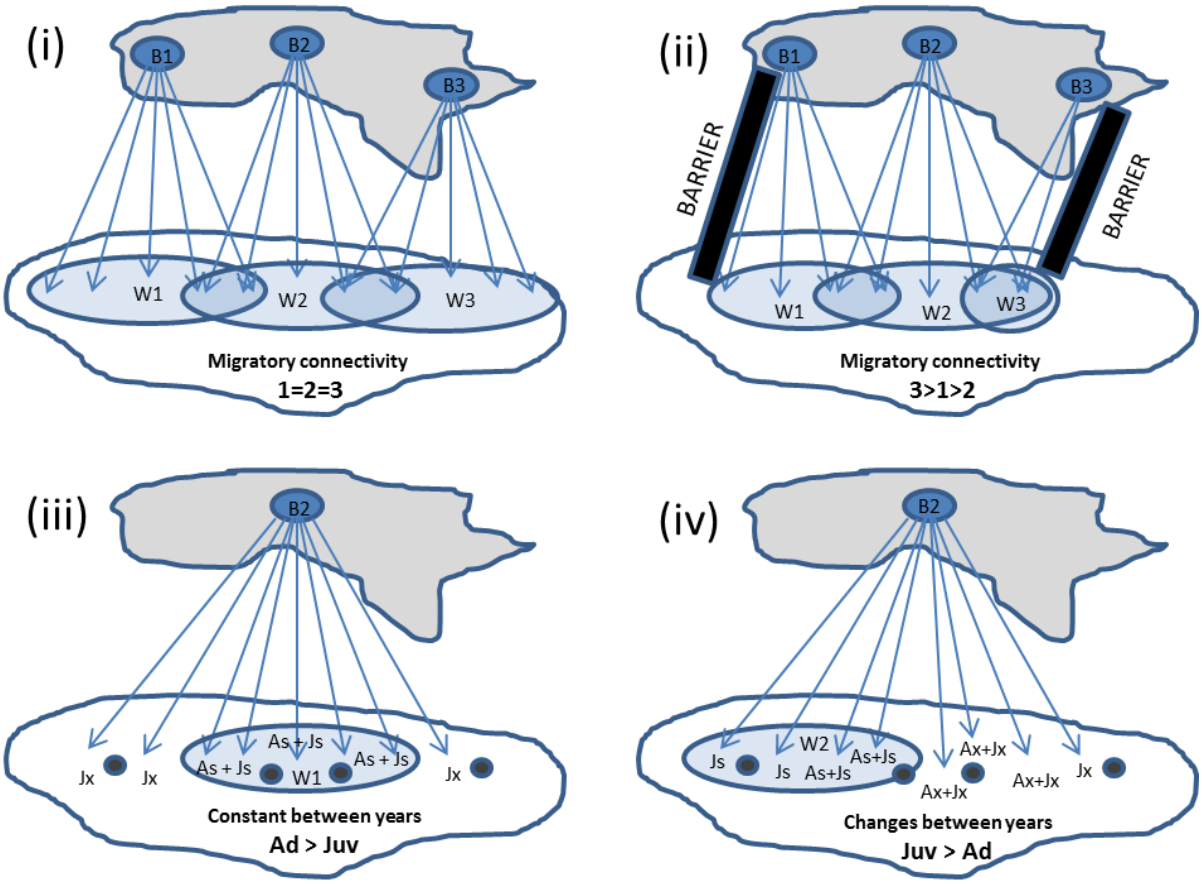


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971 Fig. 2
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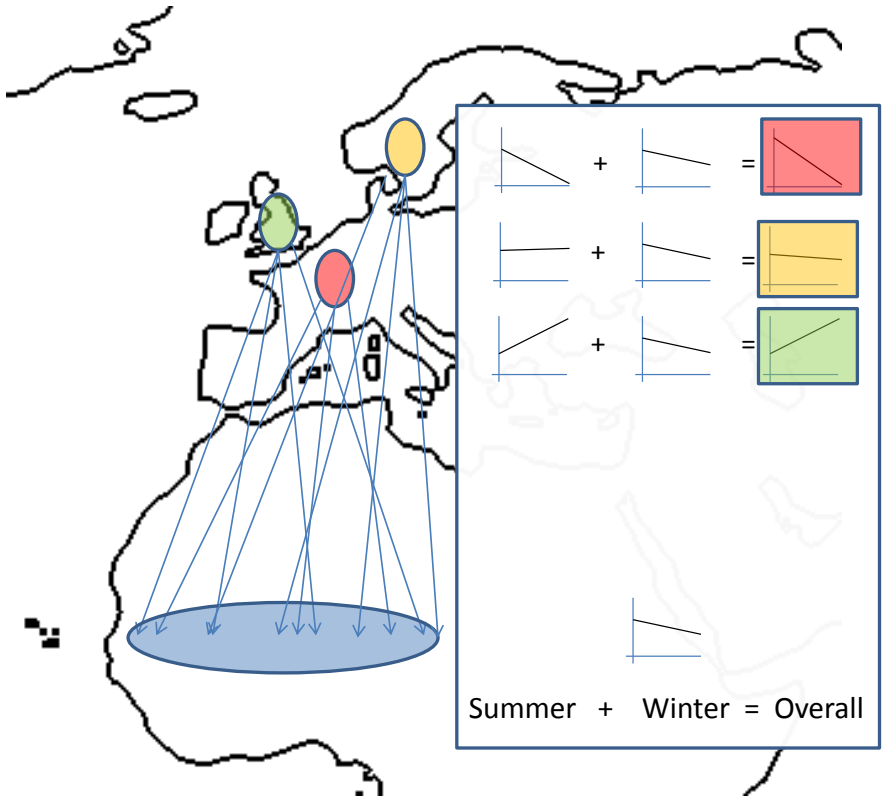


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